

Comparative Studies in the Biology of *Lycopodium carolinianum*

JAMES G. BRUCE*¹

Lycopodium carolinianum L., both temperate and tropical in distribution, occurs in North America along the Gulf and Atlantic coasts as far west as Texas and as far north as Long Island, New York. Its green, surficial gametophytes were described by Koster (1941), and Löve and Löve (1958) reported a chromosome number for it of $n=39$. Various authors have included the species in morphological or anatomical surveys of the genus, but little concerted effort has been given to a detailed study (Wilce, 1972; Chu, 1974; Øllgaard, 1975; Bruce, 1976). Ballard (1950), in his work on African *L. carolinianum*, has produced the most complete study to date.

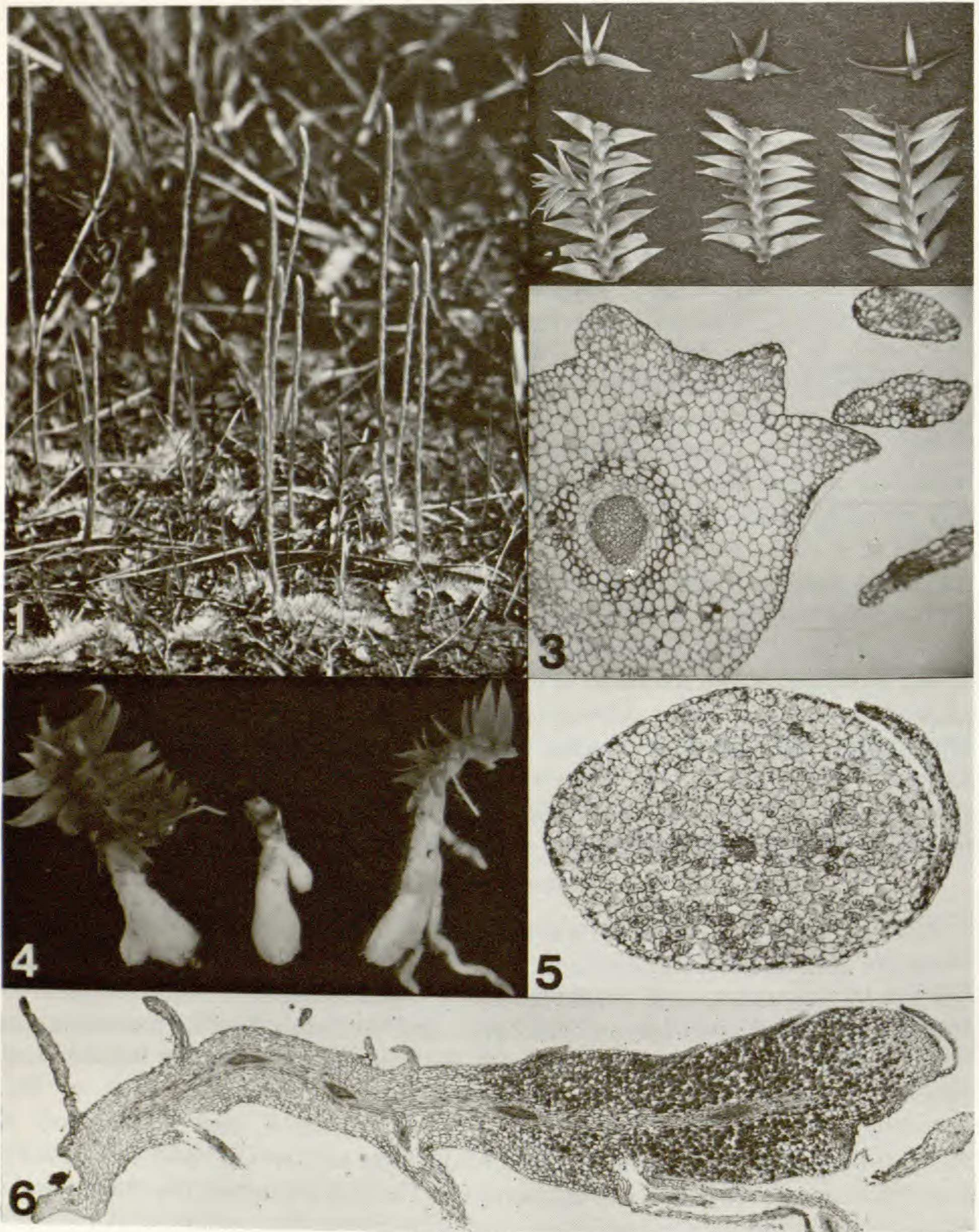
Taxonomically, several authors have treated the plant. Baker (1887, p. 28) aligned *L. carolinianum* with his subg. *Diphasium* on the basis of its distichous, dimorphous leaves. Most authors now relate it to subg. *Lepidotis*, sensu Wilce (1972). The latter association is based on habit, chromosome number, external spore morphology, and type of gametophyte. However, in confirming certain chromosome numbers in subg. *Lepidotis*, it was found that *L. carolinianum* had a number different from that reported by Löve and Löve (1958), viz. $n=35$ (Bruce, 1974). In addition, the structure of its strobilus and peduncle is different from the general condition of subg. *Lepidotis* and is like that in subg. *Lycopodium*. The latter group includes such species as *L. clavatum* L. and *L. complanatum* L. Consequently, studies were undertaken to circumscribe *L. carolinianum* both morphologically and anatomically in a more complete manner and through this to assess its relationships within the Lycopodiaceae.

MATERIALS AND METHODS

Field data from 25 localities were collected from New Jersey south and west along the coastal plain to Louisiana. Materials were preserved in FAA, FPA, or CRAF IV for anatomical preparations. Microtome sections were prepared of seven strobili, five peduncles, 12 rhizomes, and five roots. Paraffin technique was employed and sections were cut 8-15 μm in thick. These were then stained using Sharman's (1943) technique or safranin-fast green (Johansen, 1940, p. 80). Cytological material was placed into a saturated, cold, aqueous solution of paradichlorobenzene and transferred (usually after an hour) to Newcomer's solution (Newcomer, 1953) at room temperature. The vial containing the Newcomer's solution and cytological material was then transferred after an hour into a freezer until examined. The chromosomes were prepared by the squash technique and were mounted in and stained by a 1:1 solution of Hoyer's mounting medium (Beeks, 1955) and acetocarmine. The preparations were made permanent by ring-

*Department of Botany, University of Michigan, Ann Arbor, MI 48109.

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FIGS. 1-6. *Lycopodium carolinianum*. FIG. 1. Habit, $\times \frac{1}{4}$. FIG. 2. Phyllotactic patterns based upon the number of dorsal ranks of leaves. Pattern to left shows anisodichotomous branching, $\times 1.2$. FIG. 3. Mature rhizome transection, $\times 36$. FIG. 4. Rhizome tubers showing variation in shape and branching, $\times 1.8$. FIG. 5. Mature tuber transection, stele apparent as dark region in center, $\times 24$. FIG. 6. Longisection of mature tuber; the darker portion of the cortex is due to starch, $\times 6.5$.

ing the coverslip with clear fingernail polish. Dr. F. S. Wagner, University of Michigan, originally worked out this cytological technique. Photographs of both anatomical sections and cytological preparations were made on Panatomic-X film with a Zeiss Standard WL research microscope or on Tri-X or Ektapan sheet film with an Aristophot 4×5 view camera. In addition, herbarium material of *L. meridionale* Underw. & Lloyd was examined and anatomical preparations were made using Schmid's (1971, p. 13) technique.

RESULTS

Habit and habitat.—*Lycopodium carolinianum* occurs in the United States in grassy, sandy habitats along with members of the *L. alopecuroides* L. complex of subg. *Lepidotis* (Fig. 1). The most prolific development is found in open, sandy, damp borrow pits, and more or less open, broad, sandy ditches along roads.

The photosynthetic portion of the sporophyte is a prostrate shoot which branches anisodichotomously (Figs. 1 and 2). The single strobilus develops atop a thin, elongate peduncle which possesses scattered, reduced leaves (Figs. 16 and 17). Many plants are sterile and produce no strobili. New plants are formed vegetatively as the older rhizome parts decay, thereby breaking organic connection between branch shoots.

Rhizomes.—The phyllotaxy of the rhizome of *L. carolinianum* reveals three distinct patterns (Fig. 2). Two lateral ranks of broad based leaves occur so that the leading edge of one leaf underlies the trailing edge of the leaf next closest to the apex. These lateral leaves are arranged in approximate pairs. Dorsally, along the top of the stem, there may be one, two, or three ranks of smaller leaves corresponding to the three patterns. Vascular traces to the lateral leaves depart from the stele essentially parallel to the ground in all three phyllotactic types. The lateral ranks of leaves are displaced differentially depending upon the phyllotactic pattern.

The leaf primordia in the shoot apex are not all of the same size initially. The primordia of the two lateral ranks of leaves are largest and involve much of the lateral flanks of the meristematic tip. The spiral phyllotaxy, characteristic of *Lycopodium* in general, is here greatly distorted.

The mature stem consists of a central stele surrounded by a three-zoned cortex and epidermis (Fig. 3). The stele is moderately banded and surrounded by a narrow, parenchymatous cortical zone. Surrounding this parenchymatous layer is a sclerenchymatous band 3 or 4 cells thick. The bulk of the stem is composed of the large-celled parenchymatous outer cortex whose peripheral layers are chlorophyllous. A single-layered epidermis bounds the cortex. The leaves have a single, unbranched mesarch vascular strand which lacks phloem. The leaves are uniformly parenchymatous, and their cells are elongate parallel to the vein.

Tubers.—Rhizome tips may form underground, perenniating tubers in late fall (Fig. 4). In spring, the storage shoot grows to the soil surface, whereupon normal plagiotropic growth resumes. The frequency of tuber formation is relatively low. In two collections totaling 391 shoot tips, tubers were present on 18/179 (10.0%) shoot tips of one collection and 13/212 (6.1%) of the other.

Mature roots of *L. carolinianum* possess a distinctive internal structure (Fig. 13). The stele is typical of most *Lycopodium* roots with its C-shaped xylem strand. A three or four cell thick layer of thin-walled cells immediately surrounds the stele in mature roots. External to this inner cortical layer is a large, cylindrical lacuna (Figs. 10 and 13). When mature roots are placed under water, this air filled cavity is obvious through the outer cell layers. Developing roots initially have several thin-walled layers where the lacuna forms. Although air can be seen within the root often to 0.5 mm of the tip, it is due to the large intercellular spaces in the thin-walled cell zone of the cortex prior to the formation of the lacuna. At about 1.0 cm from the root tip, these cells begin to separate from each other and collapse, and the conspicuous, empty ring in the cortex of older roots becomes apparent approximately 1.0 mm from the site of the initial degeneration. Peripheral to the lacuna is the outer cortex, which is two or three cells wide. The cells of the outer cortex have thicker walls than those of the inner cortex. An epidermis is present which is not much differentiated from the outer cortex, but which produces the root hairs.

The root hairs are thin cells which protrude perpendicularly to the root axis. They are nucleate, nonseptate, and usually paired (Figs. 11 and 15). Maximum length was not determined, although there were many in excess of 1.0 mm.

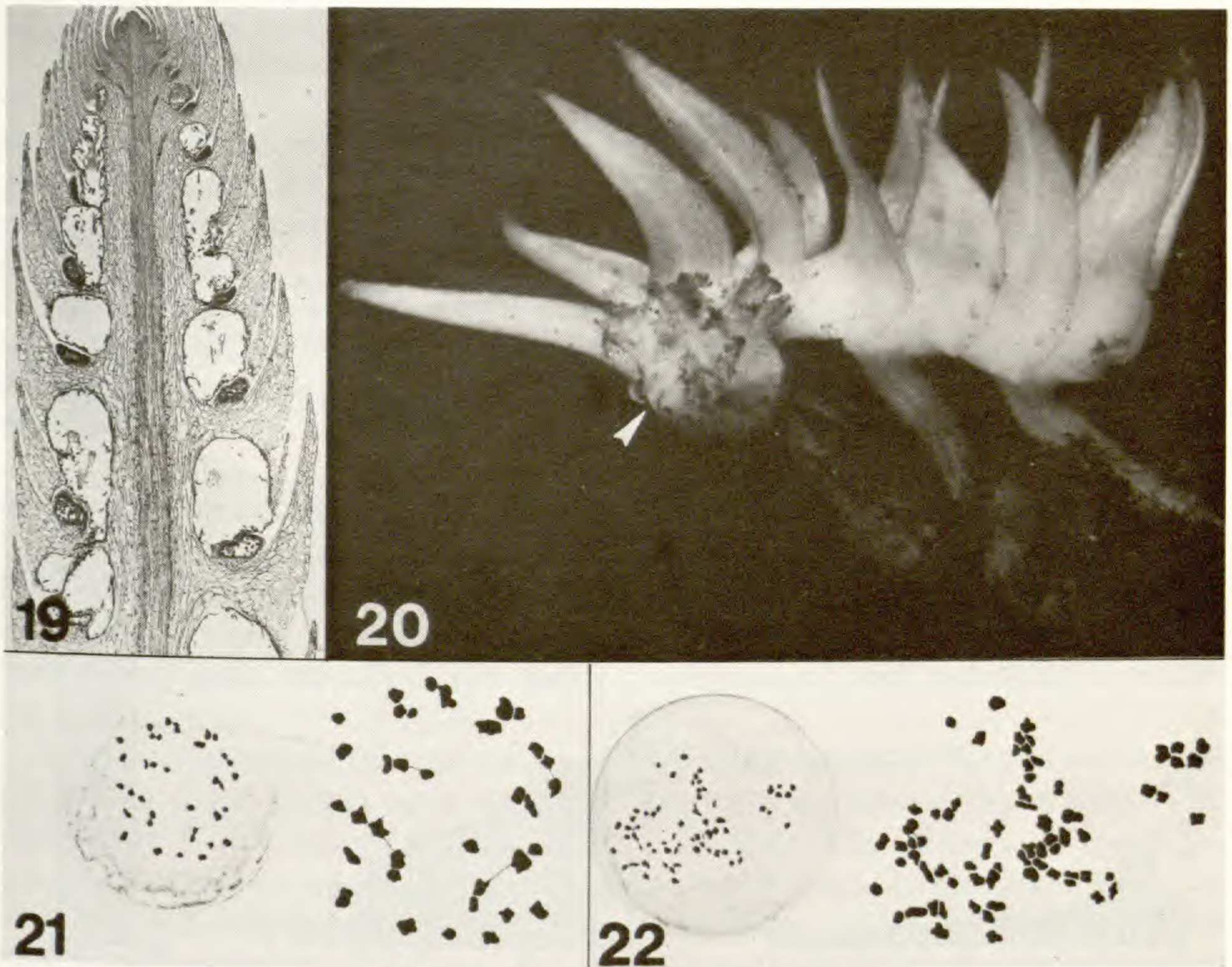
The cells of the root protoderm are produced in longitudinal files extending from near the root tip. Every other cell in the file subsequently elongates and forms a tabular cell of the root epidermis (Fig. 11). The remaining cells usually undergo an anticlinal division parallel to the line of the file. This produces two initials which then elongate perpendicularly to the root axis to form paired root hairs (Fig. 15, arrows). First evidence of root hair growth is seen approximately 0.5 mm from the tip; when the root hairs are 1.5 mm from the root tip, they are apparently fully elongate.

Peduncle and strobilus.—A single strobilus forms atop each slender, unbranched peduncle (Figs. 1, 16 and 17). In any one clone there are many sterile plants. The fertile plants usually produce only a single peduncle, which arises anisodichotomously from the dorsal side of the rhizome.

The peduncle and its reduced leaves remain green until the strobilus has fully differentiated. Internally, the peduncle is compact, with a cortex divided into three distinct zones (Fig. 18). The stele is radially symmetrical with approximately eight xylem arms alternating with the phloem. One phloem mass was observed in the center of the stele surrounded by xylem. The inner cortex adjacent to the stele consists of a layer of thin-walled cells 3 or 4 cells thick. Around this is a layer of thick-walled sclerenchyma 4-6 cells wide, which is surrounded by an outer cortex of thin-walled cells 5-8 cells wide. A single-layered epidermis covers the peduncle. Mesarch leaf traces depart from the stele at a low angle and gradually diverge through the cortex. The protoxylem in the leaf traces of the peduncle is often destroyed, producing a lacuna.

The strobilus has six vertical ranks of sporophylls in alternating whorls of three. Like the peduncle, the strobilus lacks chlorophyll when mature. The sporophylls are tightly appressed and consist of an upright, externally exposed portion and a

hidden, stalk-like portion which connects the sporophyll to the strobilar axis. The stele is similar to that of the peduncle. There is a conspicuous inner cortex of thin-walled cells. The remainder of the cortex of the mature strobilus consists of a large mucilage canal (Fig. 19). This initially forms in the stalk-like portion of the sporophyll and extends into the strobilar cortex. Connections between similar



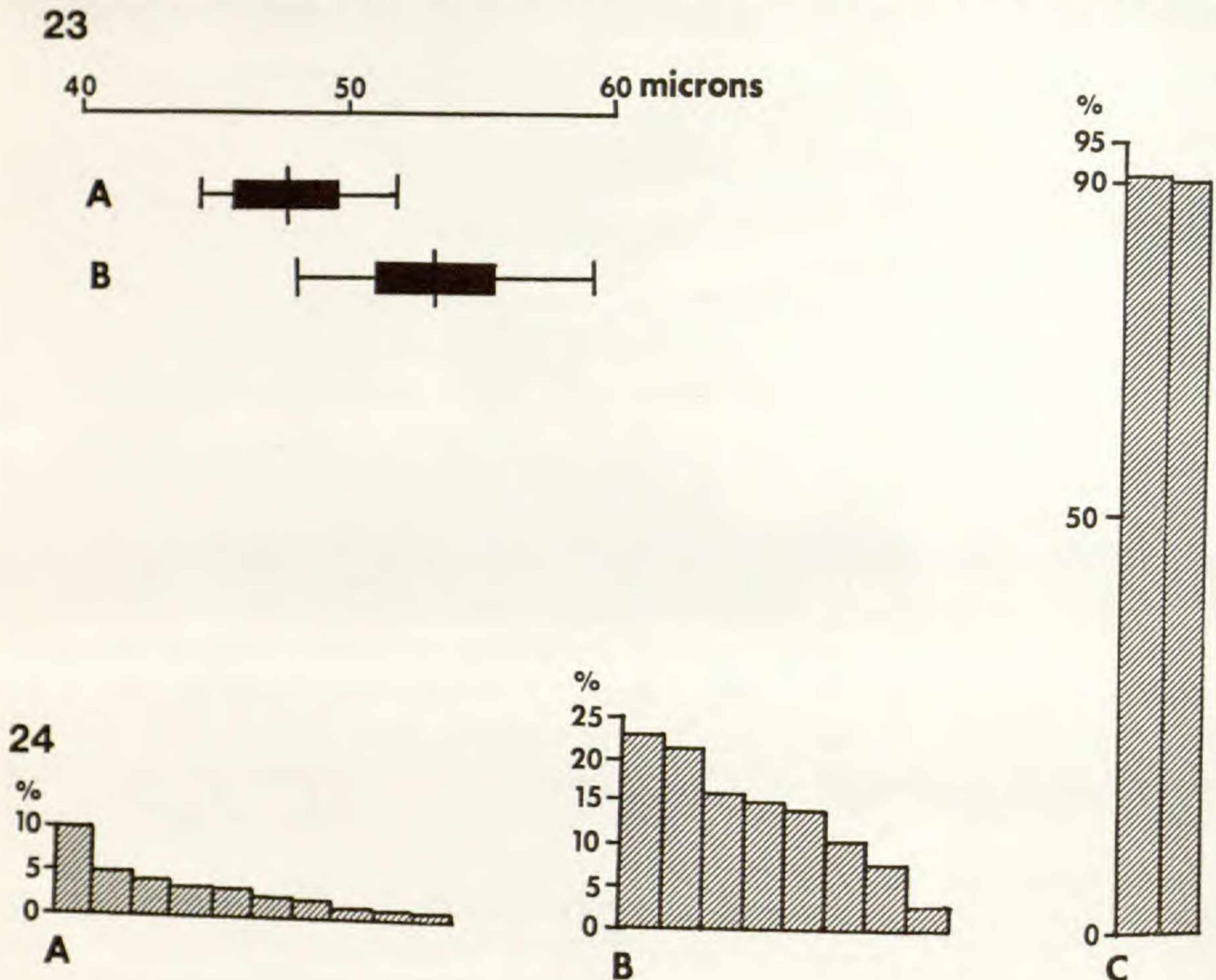
FIGS. 19-22. *Lycopodium carolinianum*. FIG. 19. Strobilus longisection with conspicuous, basal mucilage canals apparent as large clear spaces, $\times 12.5$. FIG. 20. Young sporophyte with attached gametophyte (arrow), $\times 10.5$. FIG. 21. Diploid chromosomes, $n=35$, interpretive drawing at right, first meiotic metaphase within spore mother cell wall at left. FIG. 22. Tetraploid chromosomes, $n=70$, interpretive drawing at right, first meiotic metaphase within spore mother cell wall at left.

regions of adjacent sporophylls produce a mucilaginous cylinder within the strobilus. Development and maturation of these canals has been treated more fully in Bruce (1976). The mucilage cavity does not extend into the upright, exposed portion of the sporophyll.

Chromosomes and spores.—Chromosomes were counted from one locality in North Carolina (Onslow Co., Bruce 72028) and another in Louisiana (Beauregard Pa., Bruce 73147). Several clear counts were obtained from each locality. In North Carolina, meiotic material had $n=35$ (Fig. 21). In Louisiana, a meiotic count of $n=70$ was obtained (Fig. 22). Plants from the two localities are morphologically identical, except for spore size. A count of 115 chromosomes,

based on somatic material, was obtained from additional Louisiana material in which considerable spore abortion had occurred. The chromosomes vary in size, with several somewhat larger than the others.

Spore size is bimodal and correlates with the different chromosome numbers (Fig. 23); North Carolina material has a mean of 48 μm and Louisiana material a mean of 53 μm . In addition, spore abortion percentages were determined by counting the number of deformed spores in ten samples of 100 spores for each



FIGS. 23, 24. *Lycopodium carolinianum*. FIG. 23. Spore size distribution with range, mean, and one standard deviation on either side of the mean. FIG. 24. Spore abortion percentages based on 100-spore samples. A = diploid (10 samples), B = tetraploid (8 samples), and C = triploid (2 samples).

locality (Fig. 24). The North Carolina material is fairly uniform and generally has less than 10% abortion. However, the Louisiana material revealed two distinct groups: eight samples had less than 25% spore abortion, but two samples had ca. 90% spore abortion. The strobilus from which the somatic count of 115 chromosomes was taken also had many aborted spores in its more mature sporangia.

Gametophytes.—Sixteen gametophytes, eight with attached sporophytes, were found along a ditch in Onslow Co., North Carolina, during January, 1976. Some of the sporophytes were large enough to allow identification (Fig. 20). The gametophytes were green, surficial, and consisted of a tuberous body surmounted by numerous, photosynthetic lobes. All the gametophytes came from a small area near the ditch crest and all were associated with mature *L. carolinianum*.

DISCUSSION

Several features of *L. carolinianum* suggest a relationship with either subg. *Lepidotis* or subg. *Lycopodium*. These features are summarized in *Table 1* and are discussed below.

Lycopodium carolinianum occupies the same moist habitat as many members of subg. *Lepidotis* in the Gulf and Atlantic coastal plain. Ballard (1950) points out a similar habitat for African specimens of *L. carolinianum*.

The habit of the plant, with its repeatedly dichotomous but relatively short-lived rhizomes, is similar to that of *L. inundatum* L., *L. alopecuroides*, *L. prostratum* Harper, and *L. appressum* (Chapm.) Lloyd & Underw., all of subg. *Lepidotis*. Although the rhizomes in both subg. *Urostachys* and subg. *Lycopodium* also die off from behind, Primack (1973) has shown the rhizomes of these subgenera to be more long-lived.

The rhizome has a mixture of morphological and anatomical features of both subg. *Lepidotis* and subg. *Lycopodium*. The absence of veinal mucilage canals throughout the plant combined with the presence of basal mucilage canals in the strobilus is strongly suggestive of subg. *Lycopodium* (Bruce, 1976). This is also true of the related species *L. drummondii* Spring and *L. meridionale*. Chu (1974) found the rhizome leaves in *L. carolinianum* to correspond to the leaves of subg. *Lepidotis* in characters of the epidermis, mesophyll cells, and vascular bundles. Lastly, the presence of storage tubers formed from the stem tips suggests similarity to subg. *Lepidotis*. These perenniating tubers are closely comparable to structures found in *L. alopecuroides* and *L. prostratum*, both belonging to subg. *Lepidotis*.

Ballard (1950) stated that the tubers of African lycopodiums formed toward the end of the rainy season as a means of surviving an intense dry season. The situation in North American plants seems different. The tubers are formed infrequently and always toward the end of the warm season. There is no dry season to avoid. Freezing likewise is not limiting, for many plants which do not form tubers survive winter conditions. The low, wet areas in which these plants grow, however, contain much surface litter by late winter or early spring as a result of the death of the above ground parts of grass and other plants. Thus, frequent grass fires may occur, and tuber formation in North American *L. carolinianum* may be an adaptation allowing the plants to withstand these fires.

The few papers dealing with the roots of *Lycopodium* are almost entirely restricted to histological descriptions of root origin and development (Bruchmann, 1874, 1898; Pixley, 1968; Saxelby, 1908; Stokey, 1907; Van Tiegham & Douliot, 1888). In general the roots are relatively simple in structure, with a single xylem strand that is C-shaped in cross-section in the center. The horns of the C are pointed away from the stem stele. However, in certain species the roots at their origin from the parent stele are almost indistinguishable from it (Pixley, 1968, illustrates two of these). The ultimate rootlets of these species are typical of other roots of *Lycopodium*, with their characteristic C-shaped pattern. In subgenera *Lepidotis* and *Urostachys*, the root steles are always simple C-shaped structures. However, in at least ten species of subg. *Lycopodium* (*L. alpinum* L., *L. an-*

notinum L., *L. clavatum*, *L. complanatum*, *L. deuterodensum* Herter, *L. flabelliforme* (Fern.) Blanch., *L. obscurum* L., *L. sitchense* Rupr., *L. tristachyum* Pursh, and *L. volubile* Forst.) they are the elaborate, polyarch type when they first depart from the stem stele. Furthermore, the roots of subg. *Urostachys* descend through the cortex for long distances before emerging from the plant. Thus, *L. carolinianum* with its directly emergent roots and simple, C-shaped strand pattern corresponds to the root type found in subg. *Lepidotis*.

Nägeli and Leitgeb (1868) found that the root hairs of *L. clavatum* originate by an oblique division of the young cells in the protoderm. This forms a wedge-shaped cell from the proximal portion of the protodermal cell. Further divisions in the root hair initial, which was so formed, leads to the formation of multiple hairs. The same situation was found by Leavitt (1904) in *L. annotinum*, *L. dendroideum* Klotzsch, *L. lucidulum* Michx., *L. obscurum*, *L. sabinifolium* Willd., and *L. sitchense*. Stokey (1907) found the same in *L. pithyoides* Schlecht. & Cham. However, Leavitt (1904) determined that in *L. inundatum* a straight rather than an oblique wall forms in the protodermal cell. This division splits the protodermal cell into two nearly equal components, the distal one forming the elongate epidermal cell and the proximal one elongating perpendicular to the axis to form the root hair. The condition found in *L. carolinianum* is similar to that in *L. inundatum*. This is further evidence of relationship of *L. carolinianum* to subg. *Lepidotis*.

An endodermis was not recognized. However, the conspicuous cortical lacuna apparently functions as a physical barrier to the movement of water and ions from the root stele through the cortex to the exterior of the plant. Whether this applies also to the roots of other species is unclear. Stokey (1907) states that an endodermis consisting of cells with suberized walls exists in *L. pithyoides*. Russov (1872, p. 130) observed that in *L. inundatum* and *L. selago* L. the endodermis of the root is only a single cell in thickness. Roberts and Herty (1934), in a study of the anatomy of *L. flabelliforme*, concluded that an endodermis is not readily identified. They based their conclusion on chemical tests for lignin, cutin, and other common wall constituents as well as on anatomical studies. The endodermis in *Lycopodium* needs further study.

The peduncle is a thin, sclerenchymatous organ which resembles those found in subg. *Lycopodium*. Similarly, the strobilus with its reduced, modified sporophylls is most closely paralleled in subg. *Lycopodium*. As discussed earlier, the mucilage canal distribution in the strobilus is indicative of subg. *Lycopodium*. Øllgaard (1975) has shown, however, that the thickening of the walls in the external cells of the sporangium of *L. carolinianum* is of a type restricted to subg. *Lepidotis*.

Chromosome numbers in *Lycopodium* correlate well with morphological features in defining taxonomic groups. In general, subg. *Lepidotis* has $n=78$ and subg. *Lycopodium* $n=23$ or 34 . Löve and Löve (1958) observed $n=39$ in *L. carolinianum*. This corresponds with subg. *Lepidotis*, which has exactly twice this number. However, meiotic material proved to have $n=35$. A possible explanation of this discrepancy is size variation in the chromosomes. Large chromosomes might have been interpreted as being two small chromosomes. Cytological difficulties in *Lycopodium* have been recognized for many years (Manton, 1950, p.

246). Wilce (1965) points out specifically difficulties due to size variation. I also believe this is one of the chief problems.

The count of $n=35$ in *L. carolinianum* is phenetically closer to $n=34$, the number characteristic of the *L. clavatum* group of subg. *Lycopodium*, than to $n=78$, the number characteristic of subg. *Lepidotis*.

The chromosome numbers and spore size and abortion data support an hypothesis of autotetraploidy with subsequent back-crossing to produce a sterile triploid. Plants with a chromosome number of $n=35$ and normal spores are diploids; those with of $n=70$ and larger spores, but morphologically indistinguishable otherwise, are tetraploids; those with $n=115$ and aborted spores are triploid hybrids.

TABLE 1. CHARACTER COMPARISON BETWEEN *Lycopodium carolinianum* AND SUBGENERA *Lepidotis* AND *Lycopodium*.

Character	subg. <i>Lepidotis</i>	<i>L. carolinianum</i>	subg. <i>Lycopodium</i>
Habitat	moist	moist	dry
Habit	"annual"	"annual"	3, 4, or 5 years
Leaf epidermal cell wall	straight	straight	undulate
Veinal mucilage canal	present	absent	absent
Rhizome tuber	present or absent	present or absent	absent
Root stele pattern	C-shaped	C-shaped	polyarch initially
Root hair origin	straight division?	straight division	oblique division
Peduncle leaves	like rhizome leaves	reduced, modified	reduced, modified
Sporophylls	like rhizome leaves	reduced, modified	reduced, modified
Sporangium cell walls	straight, thin and unlignified	straight, thin, and unlignified	sinuate, thin, and lignified
Spore surface	rugulate	rugulate	reticulate
Chromosome number (n)	78	35	23, 34
Gametophyte habit	surficial	surficial	subterranean
Gametophyte nutrition	hemisaprophytic	hemisaprophytic	holosaprophytic

Wilce (1972) has shown that external spore morphology closely resembles that of the *Lepidotis* group.

Koster (1941) previously reported the gametophytes of *L. carolinianum* as green and surficial. Unfortunately, he neither illustrated nor described them. They appear, based on the present collection, similar to those described for subg. *Lepidotis* (Holloway, 1916, 1920; Treub, 1884, 1888; Goebel, 1887; Chamberlain, 1917). Gametophytes of the other two subgenera are either subterranean or epiphytic.

Lycopodium carolinianum provides a mixture of features combining characteristics of subg. *Lepidotis* and subg. *Lycopodium* (Table 1). The majority of characters demonstrate a closer phenetic similarity to subg. *Lepidotis*. While *L. carolinianum* appears properly placed in subg. *Lepidotis*, its peduncle and strobilar morphology, mucilage canal arrangement, and chromosome number suggest that a new section be erected to accommodate it.

Previously, Pritzel (1900) included *L. carolinianum* in sect. *Inundata*. He divided the section into two groups, one including *L. carolinianum*, the other *L. inundatum*. The section held together primarily on habital features. The other two

sections in the subgenus, *Lateralia* and *Cernua*, are both distinct on other grounds.

Lycopodium sect. Caroliniana Bruce, sect. nov.

A sectione Inundata foliis vegetativi canalibus mucosis destitutis, pedunculo gracili et strobilo compacto ut in subgenere Lycopodio, et chromosomatum numero $x=35$ differt.

TYPE SPECIES: *Lycopodium carolinianum* L.

Other species which may prove to be included in this section are *L. drummondii*, *L. meridionale*, *L. tuberosum* A. Br. & Welw. ex Kuhn, *L. paradoxum* Mart., *L. sarcocaulon* A. Br. & Welw. ex Kuhn, and *L. carnosum* A. Silv.

On the basis of the correlated trends of mucilage canal distribution and sporophyll specialization, Bruce (1976) argued that subg. *Lycopodium* was derived from elements within subg. *Lepidotis*. The features of *L. carolinianum*, i.e., its slender peduncle and compact strobilus, its mucilage canal arrangement, and its low chromosome number, which make it somewhat anomalous in subg. *Lepidotis*, are the general condition in subg. *Lycopodium*. This suggests that *L. carolinianum* arose from along the phylogenetic line which led from subg. *Lepidotis* to subg. *Lycopodium*.

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SHORTER NOTES

A RECORD OF OPHIOGLOSSUM VULGATUM L. FOR NORTH DAKOTA.—*Ophioglossum vulgatum* L. was collected in Richland County on July 21, 1974, 3.5 miles east and 1 mile south of McLeod (*Barker 6112*, NDA). A colony of 200-300 plants was found growing in a wet prairie meadow which is dominated by *Carex lanuginosa*. In observing the vegetation, it was possible to see the outline of a formerly cultivated field. The ferns were growing along the margin of this field, which had been abandoned for at least 30 years. This species is reported for St. Louis County, Minnesota and Cherry County, Nebraska. It is interesting to note that the plant occurs in a prairie meadow in the "Nebraska sandhills" and that the site in North Dakota also is in sandhills. This record represents a disjunct population of *O. vulgatum*, which is more common in the eastern U.S.—*William T. Barker and Jon Hanson, Department of Botany, North Dakota State University, Fargo, ND 58102.*

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Manuscripts submitted to the JOURNAL are reviewed for scientific content by one or more of the editors and, often, by one or more outside reviewers as well. During the past year we have received the kind assistance of Drs. J. M. Baskin, A. M. Evans, R. H. Eyde, R. E. Holttum, R. M. King, J. H. Kirkbride, Jr., R. M. Lloyd, H. E. Robinson, W. A. Shropshire, Jr., and J. J. Wurdack. We welcome suggestions of other reviewers and offers of assistance.—D.B.L.

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